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The bracing and fusing pattern of longitudinal veins at base in living mayflies (Insecta: Ephemeroptera)

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Abstract: The bracing and merging pattern of basal longitudinal veins plays an important role in phylogeny reconstruction within Pterygota. Unfortunately, the basal venation pattern of living mayflies has changed from the ancestral state in most species, but in very rare cases, the origins of some longitudinal vein bases are preserved and visible. The wing base of *Siphluriscus chinensis* has an independent subcostal brace, partial stem of the media, visible stem of the cubitus, and indications of the origins of MA and Rs. This kind of wing base plus those of *Ephemera rufomaculata* and *Chromarcys magnifica* show the venation groundplan of modern Ephemeroptera (stem of M parallel to or fused with R basally, MA and Rs fused together for certain distance then separate, Cu independent at base). This pattern seems close to that of Neoptera while different from Odonata. In the latter, the M fused with Cu basally. The hypothesized function of subcostal brace in mayflies is to strengthen the connection between distantly separated longitudinal veins because of sclerite plate at radius vein base. This hypothesis also can be used to explain complicated and unique venation of dragonfly.

Key words: Ephemeroptera; Odonata; Neoptera; vein; wing; phylogeny; flight; dynamics

1 INTRODUCTION

The living mayfly wing base has been investigated by a number of researchers (Needham *et al*., 1935; Edmunds and Traver, 1954; Brodsky, 1970, 1974, 1994; Tsui and Peters, 1972; Pfau, 1991; Kluge, 1994, 2000; Wootton and Kukalová-Peck, 2000). Unfortunately, these studies did not concentrate their attention on origin and evolution of the main veins in the wing base, in particular those of Rs, MA, MP, CuA and CuP. The wing bases of most extant mayfly species have changed dramatically from the ancestral wings. In various evolutionary lineage representatives of mayflies studied, origination of main longitudinal veins can rarely be seen.

Fossil mayflies show diverse vein patterns. Kukalová-Peck (1985) proposed that the Carboniferous Bojophlebiidae, Syntonopteridae and Triplosobidae are mayflies or at least the ancestors of Permian Protereismatidae, which were generally considered the direct ancestors of recent mayflies (Needham *et al*., 1935; Sinitchenkova, 1984; Kukalová-Peck, 1985, 1991). Some researchers believed that the Triplosobidae may be the processor of Protereismatidae (Hennig, 1981; Sinitchenkova, 1984; Carpenter, 1992), but Kluge (1995) proposed that the larva of Bojophlebiidae sensu Kukalová-Peck was not a true mayfly.

Based on fossil and extant evidences, Kukalová-Peck (1983, 1985, 1991, 1997) provided a wing ground-plan for mayflies, dragonflies and neopterans respectively, and noted that bracing and/or fusing of a section of M (or MA) and RP (or R), Cu (or CuA) and M, RA and RP occurs in most Palaeoptera and is typical for the odonato-ephemeroid clade. However, in her hypothetical modern mayfly wing, the stems of M and Cu were hypothesized from wing base grooves instead of visible veins, because these have become desclerotized in her view. In my opinion, because of wing twisting, there are different grooves in different views of the same specimen, so they can not be used for further deduction.

Siphluriscus chinensis Ulmer (Ephemeroptera: Siphluriscidae) may originate from at least the Jurassic era, and has a large number of plesiomorphic characters in both the adult and immature stages (Zhou and Peters, 2003). This species reserves some clear longitudinal vein traces at the wing base. Based on it, a pattern of mayfly venation can be hypothesized. I compared it with additional mayfly species in other evolutionary lineages; none of them conflicted with my hypothesis and all provided further confirmation. The wing base of *S. chinensis* is described and figured

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here, as are two other typical representative species. And in my view, the basal pattern of longitudinal veins in this theory is useful to reconstruct the phylogeny between Ephemeroptera, Odonata and Neoptera, and discuss the evolution of insect flight.

2 MATERIALS EXAMINED AND TERMS

Siphluriscus chinensis Ulmer (1920): 1 ♀, Zhejiang Province, Bai-Shan-Zhu, Qingyuan county (27.37°N, 119.04°E), 20-Ⅸ-1993 leg. WU Hong; 1 ♂, Zhejiang Province, Tian-Mu-Shan mountain (30.26°N, 119.34°E), 2-Ⅵ-1999, leg. ZHAO Ming-Shui; 1 ♀ subimago, Guangxi Province, Rongshui County, Jiu-Wan Mt., Wei-Lin-Jiang forestry station, 5-Ⅷ-2003, leg. JIANG Guo-Fang (In Nanjing Normal University, China).

Ephemera rufomaculata Zhou *et* Zheng, 2003: 10 ♂♂20 ♀♀, Feng-Shan village, Jinggu county (23.45°N, 100.37°E), Yunnan province, China, leg. by ZHOU Chang-Fa on 2001-Ⅳ-8 (In Nanjing Normal University, China).

Chromarcys magnifica Navás, 1932: 3 ♀♀(in slide), THAILAND: Chiengmai Province, East Fork, Mae Ping, 21-Ⅺ-30-Ⅺ-1964, leg. W. L. and J. G. Peters (In Florida A & M University, USA).

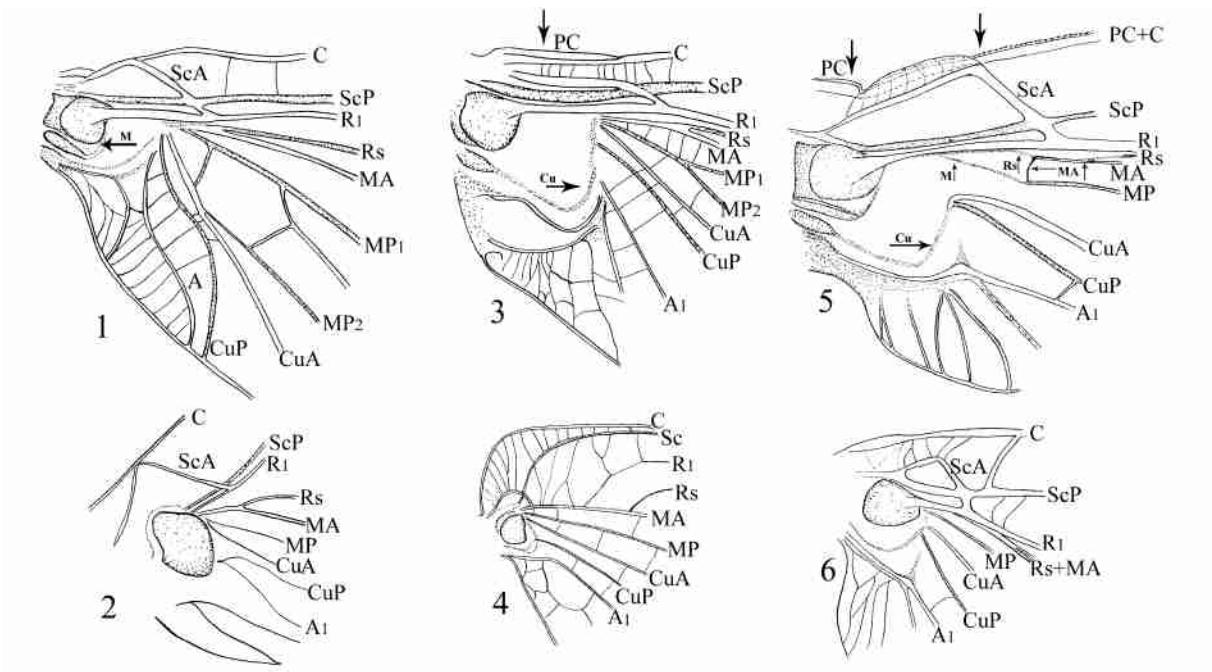
And many other species deposited in Nanjing Normal University and Florida A & M University.

Terms are followed after Kukalová-Peck (1983, 1991): precosta (PC, PCA +, PCP -), costa (C, CA +, CP -), subcoxta (Sc, ScA +, ScP -), radius (R, RA +, RP -), media (M, MA +, MP -), cubitus (Cu, CuA +, CuP -), anal (A, AA +, AP -) and jugal (J, JA +, JP -). A = anterior, P = posterior, + = convex, - = concave.

3 RESULTS

The forewing and hindwing bases of *Siphluriscus chinensis*, *Chromarcys magnifica* Navás, and *Ephemera rufomaculata* Zhou *et* Zheng are shown in Figs. 1 - 6. The characteristics of *Siphluriscus chinensis* include the following:

1) A small, serrated precostal vein (fusion of Pc, CA and CP in Kukalová-Peck, 1985) is visible anterior to the costal vein in the basal section of the wing (Figs. 5, 8, 9). Although Snodgrass (1935) thought that this condition was not present in extant insects, it is clearly indicated in *Siphluriscus chinensis* and *Chromarcys magnifica* (Fig. 3) but appears only as an anterior serration in many other mayflies (Kukalová-Peck, 1985). In the hind wing of *Siphluriscus* and other species, a precostal vein is not distinguishable.

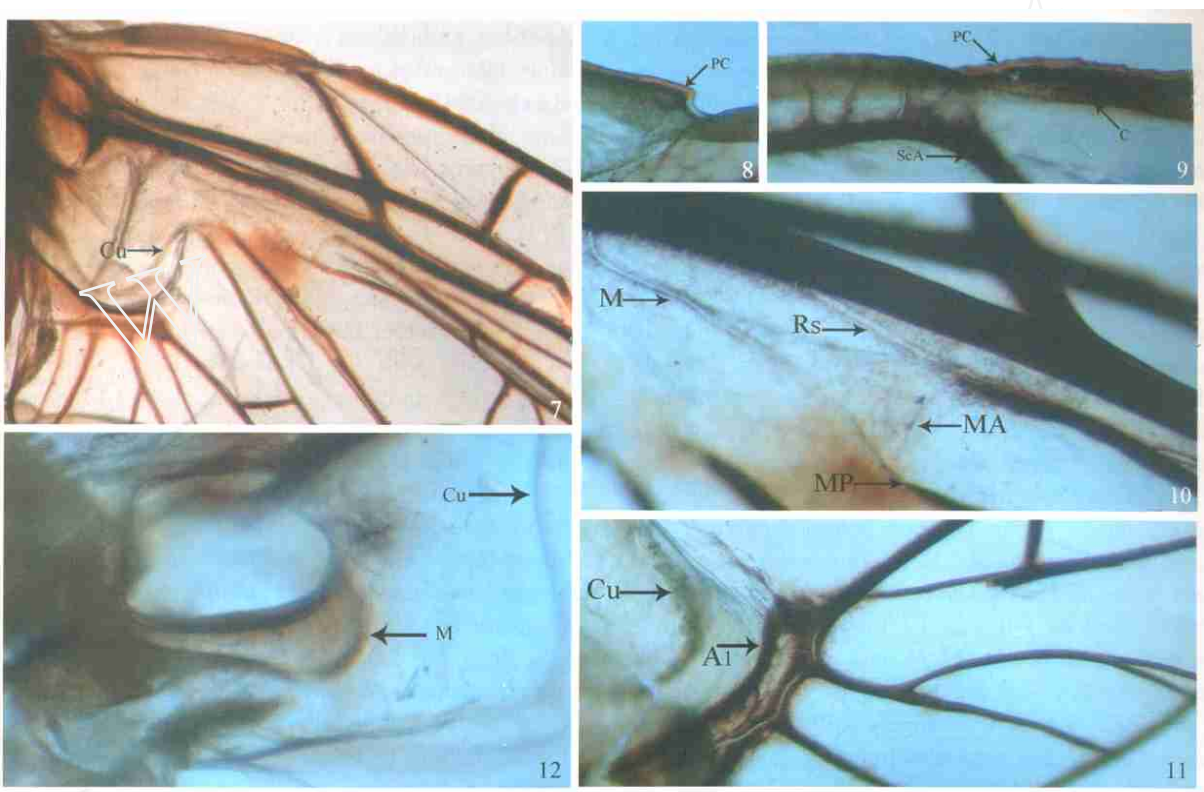


Figs. 1 - 6 The wing base of three mayfly species (dorsal view)

1 - 2. *Ephemera rufomaculata* Zhou *et* Zheng: 1. Forewing; 2. Hindwing. 3 - 4. Chromarcys magnifica Navás: 3. Forewing; 4. Hindwing. 5 - 6. *Siphluriscus chinensis* Ulmer: 5. Forewing; 6. Hindwing. Concave veins and vein traces dotted. Subcostal brace did not fused with C completely. The stem traces of Sc, R, M and Cu are clear, and that of Cu bent remarkably.

2) The subcostal brace (ScA, = ScA_{3-4}^{+} in venation pattern sensu Kukalová-Peck, 1985) does not meet the costal vein. The membranous area between ScA and C in the forewing is lightly sclerotized but cross veins are visible in the region between ScA and C (Figs. 5, 9). A similar condition is present in *Chromarcys* (Fig. 3). In most Ephemeroptera, the subcostal brace meets the costa, or the separation of the two is indistinct. In the hind wing, the subcostal brace is complete and well separated from the costa (Figs. 2, 4, 6). In many other mayflies with large hind wings, for example *Chromarcys* or *Siphlonurus mirus* (Eaton) (illustrated in Sartori and Peters, 2004), the subcostal brace is similarly expressed, although often incompletely formed.

3) The subcostal brace (ScA) separates from Sc (ScP) near the wing base (Figs. 5, 7). The stem of Sc does not fuse with R but runs parallel to it. The same is true for the hind wing and all species with clear hind wing venation.



Figs. 7 - 11　Digital photographs of wing base of *Siphluriscus chinensis* Ulmer

7. Whole view (arrow shows the position of Cu); 8. Base of PC and C; 9. PC, C and ScA (showing that ScA does not fuse with PC + C); 10. Base of Rs, stem of M, MA and MP; 11. Cu and A; 12. Wingbase of *Ephemera rufomaculata* (showing the stems of M and Cu).

4) R_1 and Rs (RA and RP of Kukalová-Peck, 1985) appear to have a common stem or to be fused basally; then, after separation from R, RP is desclerotized for some distance before and after joining with MA (Figs. 5, 10). In the hind wing, RP joins MA distal to the subcostal brace (Fig. 6). In other species studied, the separation of RP from RA is indistinct, and RP never reaches the subcostal brace.

5) MA and MP diverge from the stem of M, the basal section of M is weak but clear (Figs. 5, 10). The stem of M is present and visible for much of its length. In the hind wing, MA and RA are separate but approximate each other distal to the subcostal brace (Fig. 6). This hind wing condition is highly variable in other mayflies.

6) CuA and CuP have a common, long, curved stem in the forewing and hind wing (Figs. 5, 6, 7, 11). The forewing condition is characteristic of all mayflies studied, but the Cu stem is variously reduced in other hind wings.

7) The stem of the anal vein is almost straight. In the forewing, only a small prong may or may not represent the remains of AA1 reaching toward CuP. In the hind wing, this vein prong reaches CuP. The condition is highly variable in other mayflies.

4　DISCUSSION

The basal vein of *Siphluriscus chinensis* supports the longitudinal-vein's pattern in ground-plan of insect wing venation sensu Kukalová-Peck (1983, 1991). The subcostal brace fusing with C is a derived character

because it is separate from C in *Siphluriscus chinensis* and *Chromarcys magnifica*, but fuses with C in most modern species. In addition, the anterior sector of each pair of longitudinal veins (Sc, R, M, Cu) is convex, the posterior sector is concave, and they have a common stem in mayflies.

In the former studies using only modern mayflies, the origin and interrelations of R1, Rs, MA, MP, CuA and CuP were not clearly indicated, although some figures in some previous literatures showed this condition to some degree (see Fig. 1 of Kluge, 1994; Fig. 53A of Kluge, 2000). Wootton and Kukalová-Peck (2000) described and figured the wing of *Ephemera danica* showing the costal and subcostal veins, together with the RA, forming a strongly three-dimensional leading-edge spar. In this figure, four other longitudinal veins (stem of RP + MA, MP, CuA and CuP) radiate almost from a single point. In the forewings of *Siphluriscus chinensis*, the stem of MA and MP appears to originate in or near R; then M and R separate into two veins (R1 and Rs, MA and MP respectively); and finally MA joins with Rs. The origin of the MA and MP stem can not be seen in most species, but in *Ephemera rufomaculata*, it is visible coming from the basal sclerites (Figs. 1, 12). After that, it bends forwards dramatically; in *Siphluriscus chinensis* Ulmer, it can be seen before separating into MA and MP (Figs. 5, 7, 10). Thus, the progressive pattern of the media vein (after issuing from the base) is hypothesized as follows: 1) fusing with or running close to the stem of R; 2) M and R separate; 3) M detached into MA and MP as well as R detached into R1 and Rs; 4) MA connects with Rs for some distance, and 5) MA separates from MP completely (as in hindwing of *Siphluriscus chinensis*). The first two points has been shown in the figures of Kukalová-Peck (1983, 1997).

In Ephemeroptera, M (stem of MA and MP) always joins with or runs along R for some distance, but M (MA or MP) never joins Cu at the base. The stem of CuA and CuP of several species (in particular *Siphluriscus chinensis*, *Ephemera rufomaculata* and some species in Siphlonuridae) and the M stem of *Ephemera rufomaculata* are clear. Kukalová-Peck (1985) reported that vein fusion between MA and RP plus CuA and M are typical ephemeroid pattern. From the present study, it is clear that the former may be, but the latter may not be. Some fossil insects, in particular those have fused or strutted CuA and M require further research to see whether they or some members of them are real mayflies or not. Maybe some of them are only the precursor of Ephemeroptera. Kukalová-Peck (1997) modified her previous synapomorphies of Palaeoptera to the following: the stem of M; the stem of Cu, simple CuP; three important braces: rp-ma, m-cu, and cup-aa1; a long curved anal brace. In my present study, the brace between m-cu is not supported as one of the synapomorphies.

The interrelationships of three winged insect clades (Ephemeroptera, Odonata and Neoptera) have been debated for many years, and all possible suggestions have been proposed (Hennig, 1981; Kristensen, 1981, 1991; Soldán, 1997), but none of the arguments can be accepted generally, even the molecular evidences did not provide similar results (Giribet and Ribera, 2000; Wheeler *et al*., 2001; Hovmöller *et al*., 2002; Ogden and Whiting, 2003; Kjer, 2004; Ogden *et al*., 2005).

More recently, most autapomorphies of modern Palaeoptera (Ephemeroptera + Odonata) are based on wing basal sclerites and veins (Kukalová-Peck, 1983, 1991, 1997). In Odonata, the basalare, fulcalare and axalare of PC and C are fused into an anterior articular plate, columns of sclerites of Sc, R, M, Cu, A and J are fused together into a posterior plate, and the stem of M is fused with Cu (Kukalová-Peck, 1983, 1991, 1997; Riek and Kukalová-Peck, 1984). In Neoptera, which have the ability to fold their wings, some sclerites of Sc, R and M have fused together into 1Ax and 2Ax, so that R and M are also fused or in extreme proximity (Kukalová-Peck, 1985, 1991). The present study shows that R and M of mayflies are also fused together or run in close proximity. This pattern is similar to Neoptera but different from Odonata.

In flying wings, R serves as an axial vein and is always strong and convex (Kukalová-Peck, 1983). Because the neopterans and mayflies have a similar fusion pattern between R and M, they might adopt similar aerodynamic system in flying because "brief fusion of veins appears often to be an adaptation to local torsion of part of the wing" (Wootton and Kukalová-Peck, 2000). Therefore, they maybe share the similar evolutionary trend: MP to A in forewings changed dramatically and showed diverse venations; hindwings small or even lost except those being used to fly. However, in dragonflies, M is fused with Cu at base and the wings differ from those of mayflies and neopterans: two pairs of wings are at the same size (Zygoptera) or hindwings larger (Anisoptera), and show somewhat uniform venations (only three kinds of wings founded in Odonata so far). The wing aerodynamics and flight movements of dragonflies are not similar to flies or bees either (Sun, 2004).

The presence of the subcostal brace (originated from ScA) is a typical character of mayfly wings. What is the function of it? Wootton (1992) pointed out that in wings or areas of wings that are corrugated with abundant cross-veins, longitudinal veins may often function not in isolation but as components of trusses,

or lattice-girders. Wootton and Kukalová-Peck (2000) pointed out that spar of costal, subcostal and RA stiffened by the ScA. Brodsky (1994) noted that "the costal brace serves to shorten the costal edge of the wing during the downstroke rather than to strengthen it." In my own view, the Brodsky's suggestion may be the effect and result of the connecting of C, Sc and R1 with costal brace and making them move as a whole. In addition, the fusion between Rs and MA and the connections of the main longitudinal veins by means of the subcostal and anal braces allow them to move together during flight. Further, if considering the large basal wing sclerites of mayflies or dragonflies and their complicated venations together, it can be deduced that the subcostal brace of mayflies and all unique structures of dragonflies may serve to connect the main longitudinal veins which are separated by the sclerites at base.

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References

Brodsky AK, 1970. Organization of the flight system of *Ephemera vulgata* L. (Ephemeroptera). *Entomologicheskoe Obozrenie*, 49: 307 - 315 (In Russian).

Brodsky AK, 1974. Evolution of the wing apparatus in the Ephemeroptera. *Entomologicheskoe Obozrenie*, 53: 291 - 303 (In Russian).

Brodsky AK, 1994. The Evolution of Insect Flight. Oxford: Oxford University Press. 229 pp.

Carpenter FM, 1992. Superclass Hexapoda. (4) Arthropoda 4. In: Moore RC, Kaesler RL eds. Treatise on Invertebrate Paleontology. Colorado: Geological Society of America and University of Kansas. 17 - 25.

Edmunds GF, Traver JR, 1954. The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. *Journal of the Washington Academy of Sciences*, 44: 390 - 400.

Giribet G, Ribera C, 2000. A review of arthropod phylogeny: new data based on ribosomal DNA sequences and direct character optimization. *Cladistics*, 16: 204 - 223.

Hennig W, 1981. Insect Phylogeny (Translated and edited by Pont AC). Chichester: John Wiley and Sons. 514 pp.

Hovmöller R, Pape T, Källersjö M, 2002. The Palaeoptera problem: basal pterygote phylogeny inferred from 18S and 28S rDNA sequences. *Cladistics*, 18: 313 - 323.

Kjer K, 2004. Aligned 18S and insect phylogeny. *Systematic Biology*, 53: 506 - 514.

Kluge NJ, 1994. Pterothorax structure of mayflies (Ephemeroptera) and its use in systematics. *Bulletin de la Société entomologique de France*, 99: 41 - 61.

Kluge NJ, 1995. A new suborder of Thysanura for the Carboniferous insect originally described as larva of *Bojophlebia*, with comments on characters of the orders Thysanura and Ephemeroptera. *Zoosystematic Rossia*, 4: 71 - 75.

Kluge NJ, 2000. Modern Systematics of Insects. Part I. Principles of Systematics of Living Organisms and General System of Insects with Classification of Primary Wingless and Palepterous Insects. Lan', St-Petersburg. 336 pp. (In Russian).

Kristensen NP, 1981. Phylogeny of insect order. *Annual Review of Entomology*, 26: 135 - 157.

Kristensen NP, 1991. Phylogeny of extant hexapods. In: Naumann ID, Carne PB, Lawrence JF, Nielsen ES, Spradberry JP, Taylor RW, Whitten MJ, Littlejohn MJ eds. The Insects of Australia: A Textbook for Students and Research Workers. Melbourne: Melbourne Univ. Press. 125 - 140.

Kukalová-Peck J, 1983. Origin of the insect wing and wing articulation from the arthropodan leg. *Canadian Journal of Zoology*, 61: 1 618 - 1 669.

Kukalová-Peck J, 1985. Ephemeroid wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemerida). *Canadian Journal of Zoology*, 63: 933 - 955.

Kukalová-Peck J, 1991. Fossil history and the evolution of hexapod structures. In: Naumann ID, Carne PB, Lawrence JF, Nielsen ES, Spradberry JP, Taylor RW, Whitten MJ, Littlejohn MJ eds. The Insects of Australia: A Textbook for Students and Research Workers. Melbourne: Melbourne Univ. Press. 141 - 179.

Kukalová-Peck J, 1997. Arthropod phylogeny and 'basal' morphological structures. In: Fortey RA, Thomas RH eds. Arthropod Relationships. London: Chapman and Hall Press. 249 - 268.

Needham JG, Traver JR, Hsu YC, 1935. The Biology of Mayflies, with a Systematic Account of North American Species. New York: Comstock Publication, Ithaca. 759 pp., 168 Figs., plates I - XI

Ogden TH, Whiting MF, 2003. The problem with "the Paleoptera problem:" sense and sensitivity. *Cladistics*, 19: 432 - 442.

Ogden TH, Whiting MF, Wheeler WC, 2005. Poor taxon sampling, poor character sampling, and non-repeatable analyses of a contrived dataset do not provide a more credible estimate of insect phylogeny: a reply to Kjer. *Cladistics*, 21: 295 - 302.

Pfau HK, 1991. Contributions of functional morphology to the phylogenetic systematic of Odonata. *Advances in Odonatology*, 5: 109 - 141.

Riek EF, Kukalová-Peck J, 1984. A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Canadian Journal of Zoology*, 62: 1 150 - 1 166.

Sartori M, Peters JG, 2004. Redescription of the type of *Siphlonurus davidi* (Navás, 1932) (Ephemeroptera: Siphlonuridae). *Zootaxa*, 469: 1 - 6.

Sinitchenkova ND, 1984. The Mesozoic mayflies (Ephemeroptera) with special reference to their ecology. In: Landa V, Soldán T, Tonner T eds. Proceedings of 4th International Conference of Ephemeroptera. Prague, Czechoslovakia, Czechoslovak Academy of Sciences. 61 - 66.

Snodgrass RE, 1935. Principles of Insect Morphology. New York and London: McGraw-Hill Book Co., Inc. 667 pp.

Soldán T, 1997. The Ephemeroptera: whose sister-group are they? In: Landolt P, Sartori M eds. Ephemeroptera and Plecoptera: Biology-Ecology-Systematic. Fribourg: MTL-Mauron + Tinguely and Lachat Sa. 514 - 519.

Sun M, 2004. How do the insects fly? *Mechanics and Practice*, 26 (1): 80 - 83. [孙茂, 2004. 昆虫是如何飞行的. 力学与实践, 26 (1): 80 - 83]

Tsui PTP, Peters WL, 1972. The comparative morphology of the thorax of selected genera of the Leptophlebiidae (Ephemeroptera). *Journal of Zoology*, 168: 309 - 367.

Wheeler WC, Whiting M, Wheeler QD, Carpenter JM, 2001. The phylogeny of the extant hexapod orders. *Cladistics*, 17: 113 - 169.

Wootton RJ, 1992. Functional morphology of insect wings. *Annual Review of Entomology*, 37: 113 - 140.

Wootton RJ, Kukalová-Peck J, 2000. Flight adaptations in Palaeozoic Palaeoptera (Insecta). *Biological Reviews*, 75: 129 - 167.

Zhou C-F, Peters JC, 2003. The nymph of *Siphluriscus chinensis* and additional imaginal description: a living mayfly with Jurassic origins (Siphluriscidae new family: Ephemeroptera). *Florida Entomologist*, 86: 345 - 352.

(责任编辑:袁德成)

现存蜉蝣翅基纵脉走向及愈合模式
(昆虫纲:蜉蝣目)

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摘要:有翅昆虫翅基纵脉的走向及愈合模式在系统发育重建中占有重要地位。然而,现存蜉蝣翅基纵脉的走向及愈合状况在大部分种类变化极大,无法推测其原始状况,只在极少数种类保留有部分可见残迹。中国拟短丝蜉 *Siphluriscus chinensis* 的翅基保留有独立的亚前缘脉弓、部分中脉 M 和肘脉 Cu 主干以及前中脉 MA 及径分脉 Rs 的走向痕迹。据此并结合红斑蜉 *Ephemera rufomaculata* 和大网脉蜉 *Chromarcys magnifica* 翅基的相关特征,本文提出了蜉蝣目主要纵脉基部走向及愈合的基本模式,其要点有:中脉主干在基部与径脉主干独自发出后先接近或愈合后又分离、它们各自分成两支后的前中脉及径分脉又先愈合再分离、肘脉始终独立。这种中脉与径脉先接近或愈合后分离的模式非常接近新翅类的情况而与蜻蜓很不相同(在蜻蜓,中脉与肘脉在基部愈合)。亚前缘脉弓的作用相信是加强了因翅基骨板发达而相互远离的纵脉间的连结作用。这个假说也可以来解释蜻蜓复杂脉相的形成原因。

关键词:蜉蝣;蜻蜓;新翅类;翅;翅脉;系统发育;飞行;动力学
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